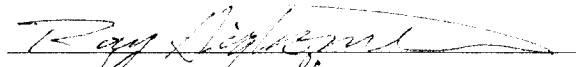




Chemosensory responses and foraging behavior of *Pycnopodia helianthoides*:
predator or scavenger?


By

Reid Sinclair Brewer


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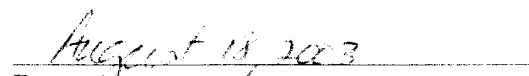

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CHEMOSENSORY RESPONSES AND FORAGING BEHAVIOR OF *PYCNOPODIA*
HELIANTHOIDES: PREDATOR OR SCAVENGER?

A

THESIS

Presented to the Faculty
of the University of Alaska Fairbanks
in Partial Fulfillment of the Requirements
for the Degree of

MASTER OF SCIENCE

By

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ABSTRACT

Chemical cues released by damaged or dead organisms can affect how and where benthic scavengers feed, whether damage or mortality is natural or fishery-related. These cues may also cause predators to act as facultative scavengers. Experiments were performed to determine the role that the seastar *Pycnopodia helianthoides* plays in the presence of scavengable prey. The results of these experiments suggest that *P. helianthoides* preferentially scavenge in lieu of its normal predatory role. When given a choice, *P. helianthoides* choose damaged or decaying food over live prey even when live prey is encountered en route to the damaged animal. The densities and activities of *P. helianthoides* were compared between areas where food was continually introduced and areas where food was not introduced. Adding scavengable food to areas with *P. helianthoides* caused a spatial redistribution of the seastar population, a change in the foraging dynamics of the seastars, and in some cases, a change in the densities of the prey that *P. helianthoides* normally consume. The effects of introducing food appeared to result in a change in the role that *P. helianthoides* plays in the benthic community. This change in modes could have significant effects on the equilibrium of the benthic community.

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INTRODUCTION

Seastars are among the most important predators in marine systems (Mauzey *et al* 1968, Paine 1974, Jangoux 1982, Duggins 1983, Shivji *et al* 1983, Dayton *et al* 1995). Several seastar species are thought to be the controlling force in benthic communities due to their large appetite and ability to find food quickly. Aggregations of seastars have been shown to cause the destruction of food sources (Mauzey *et al* 1968, Paul and Feder 1975, Warner 1979, Flagg and Malouf 1983, Shivji *et al* 1983, Pearse and Hines 1987, Ross *et al* 2002). In some areas, seastars cause patchiness in urchin populations, which may in turn affect algal growth (Duggins 1983). Elsewhere, predation by seastars has been shown to be the leading cause of juvenile (Ross *et al* 2002) and adult (Flagg and Malouf 1983) bivalve loss, and in some instances, seastars have been shown to act as keystone species, having direct control over the equilibrium of the community (Paine 1974).

Along the Pacific coast, *Pycnopodia helianthoides* is considered to be one of the most active and voracious invertebrate predators in the benthic community. In California, *P. helianthoides* may be responsible for large decreases in echinoid (*Strongylocentrotus* spp.) (Pearse and Hines 1987) and gastropod (*Calliostoma ligatum*, *Tegula pulligo*) (Herrlinger 1983) populations. In Washington, *P. helianthoides* have been observed as important predators of echinoids (*Strongylocentrotus* spp.) (Mauzey *et al* 1968). In British Columbia, *P. helianthoides* are important predators on bivalves *Saxidomus giganteus* (Lambert 1981), gastropods (*Tegula pulligo*) (Shivji *et al* 1983) and echinoids (*Strongylocentrotus* spp.) (Breen 1979). In Alaska, *P. helianthoides* may have significant impacts on several bivalve populations (*Mytilus trossulus*, *S. giganteus* and *Protothaca staminea*) (Paul and Feder 1975).

In addition to having direct limiting effects on prey organisms, *Pycnopodia helianthoides* may have overlapping diets with other predators. In southern California and southern Alaska, *P. helianthoides* and the sea otter (*Enhydra lutris*) both prey on bivalves and echinoids (Herrlinger 1983). In western Alaska, *P. helianthoides*' diet of

bivalves overlaps that of the Pacific walrus (*Odobenus rosmarus*) (Fukuyama and Oliver 1985). In either case, there may not necessarily be direct competition for food, but rather an indirect effect caused by what one organism takes out of the system. Because *P. helianthoides* focus on small prey organisms (Paul and Feder 1975), they may be affecting the number of individuals that reach the large size classes normally taken by other predators (Ross *et al* 2002).

Although the direct and indirect impacts of *Pycnopodia helianthoides*, as a predator, have been well documented, other aspects of *P. helianthoides*' feeding strategy remain unclear. Many authors suggest *P. helianthoides* are generalist predators that sweep across the seafloor ingesting anything within their paths (Mauzey *et al* 1968, Wobber 1975, Moitsoza and Phillips 1979, Sloan 1980, Lambert 1981, Herrlinger 1983, Shivji *et al* 1983, Weightman and Arsenault 2002). Despite reported observations of *P. helianthoides* feeding on many different types of carrion such as opalescent squid (*Loligo opalescens*) (Wobber 1973), seabirds (Alcidae) (Shivji *et al* 1983), spiny dog-fish (*Squalus acanthias*) (Shivji *et al* 1983), Pacific herring (*Clupea pallasii*) (Shivji *et al* 1983), ochre seastars (*Pisaster ochraceus*) (Herrlinger 1983, Shivji *et al* 1983), Pacific octopus (*Enteroctopus dofleini*) (Shivji *et al* 1983), Pacific hake (*Merluccius productus*) (Herrlinger 1983), and sea otters (*Enhydra lutris*) (personal observation), no quantitative studies have been published to establish *P. helianthoides* as a scavenger. To understand the role that *P. helianthoides* plays as a scavenger, the emphasis of this study was to evaluate the chemosensory abilities and foraging activities of these seastars in the presence of scavengable (damaged or decaying) food.

Pycnopodia helianthoides are the largest and most active seastars on the Pacific coast (Paul and Feder 1975) with a maximum diameter of 1.5 m and weighing up to 5 kg (Lambert 1941). This seastar moves using approximately 22,000 tube feet (Mauzey *et al* 1968) at a rate up to 1.5 m/min (Lambert 1981). *Pycnopodia helianthoides*, as predators, will feed intra-orally on any organism that will fit inside their oral opening and extra-orally on larger prey items. Venerid clams, such as *Saxidomus giganteus*, are common prey items of *P. helianthoides*. When these large bivalves are encountered, *P.*

helianthoides excavate up to 23 cm into the sediment to reach the bivalve, orient the bivalve under the oral opening and pull the valves slightly apart using suction exerted by the tube feet and musculature of the articulating dermal ossicles (Lambert 1981). Once the valves gape, *P. helianthoides* will extra-orally digest the bivalve by extruding its stomach into the bivalve's mantle cavity and liquefying the soft tissues with digestive secretions. Adult *P. helianthoides* can each consume up to 28.8 kg wet weight of prey/year (Breen 1979). Because of *P. helianthoides*' abundance, mobility and feeding rate, understanding the prey detecting sensory abilities and foraging techniques of these organisms will give insight into their role as scavengers in the benthic community.

Chemosensory ability is considered to be one of the most important means by which scavengers locate food. Both predators and scavengers depend on the perception of food to orient their movements towards the food source (Moitzoa and Phillips 1979, Himmelman 1988, Lapointe and Sainte-Marie 1992). The ability to chemically sense has been studied in many invertebrate groups including nematodes (Krieger and Breer 1999, Troemel 1999), polychaetes (Jensen 1992), marine gastropods (Shumway *et al* 1993, Rochette *et al* 1997, Bryan *et al* 1997), decapod crabs (Miller 1990, Gleeson *et al* 1994, Moore and Howarth 1996, Zhou and Shirley 1997, Finelli *et al* 2000), and seastars (Feder and Christensen 1966, Ferguson 1971, Swenson and McClintock 1998, Weissberger 1999, Weightman and Arsenault 2002) amongst others. Because radially symmetrical animals can receive chemical cues from all directions equally well, seastars should be an ideal shape for chemosensory perception. This contention is supported by Ferguson (1971), who showed that seastars receive net benefits from chemicals in their environment that aid in food detection. Seastars can use a tactile discriminatory ability, but are more motivated by chemical cues than by physical shapes (Sloan and Campbell 1982). The tube feet of seastars, which are extensions of the body wall, have partial function as sensory organs, with the outer tips modified exclusively for sensory function (MacGinitie and MacGinitie 1949, Valentincic 1983).

The specific role of chemosensory abilities in *Pycnopodia helianthoides*' foraging strategy is a subject of much debate. *Pycnopodia helianthoides* has been labeled

chemotactile by Herrlinger (1983), who states that these seastars feed mainly by coming into contact with prey organisms and that distance chemosensory abilities do not play a key role in foraging. Other studies suggest that *P. helianthoides* probably do use distance chemoreception as the primary means of locating food (Greer 1961, Moitzoa and Phillips 1979); however, no studies have established the use of chemoreceptive abilities or the role such an ability plays in the foraging techniques used by *P. helianthoides* or the resulting effects on the community.

The overall objective of this study was to determine if *Pycnopodia helianthoides* utilize chemosensory abilities, to what extent these abilities affect *P. helianthoides*' foraging techniques, and the effects of changing foraging roles on the associated benthic community. To examine these abilities and techniques, I used a combination of direct observations and field experiments addressing three time frames: < 1 hour, < 4 weeks, and > 1 year. Three hypotheses were posed on the immediate responses of *P. helianthoides* to prey cues (< 1 hour): (H₁) *P. helianthoides* use chemoreception to actively pursue introduced prey cues; (H₂) *P. helianthoides* must be located down-current of an introduced prey cue to detect, move to and reach the cue; (H₃) *P. helianthoides* will bypass live prey to reach damaged prey. One hypothesis was posed on the short-term effects of introducing prey cues (< 4 weeks): (H₄) *P. helianthoides* will switch foraging modes from predator to scavenger when scavengable prey is readily available. One hypothesis was posed on the chronic or long-term effects of adding prey cues to a location (> 1 year): (H₅) Local populations of *P. helianthoides* in areas where scavengable prey is consistently available will adopt a full-time scavenging role. Lastly, a hypothesis was posed on the overall role that *P. helianthoides* plays in the benthic community: (H₆) If scavengable prey is introduced into the environment, *P. helianthoides* will scavenge, forgoing live prey that it normally consumes, and thus reduce predation pressure on them.

METHODS AND MATERIALS

General

Study sites were located near the University of Alaska Fairbanks' Kasitsna Bay Laboratory in Kachemak Bay, south central Alaska, at water depths between 5 and 20 meters (Figure 1). To address hypotheses, experiments were designed to test the immediate (choice experiments), short-term (supplemental food experiment) and long-term (supplementation survey) effects of introducing scavengable food to populations of *Pycnopodia helianthoides*. The results of these experiments give insight into the sensory abilities and resulting foraging techniques used by *P. helianthoides*, as well as the effect of these organisms on the benthic community.

Choice experiments (Immediate effects)

The chemosensory abilities and foraging techniques of *Pycnopodia helianthoides* were observed in three types of choice experiments: Y-maze, cue propagation, and corridor. Each experiment was designed to observe a key component of *P. helianthoides*' feeding behavior related to the hypotheses stated above.

All of the choice experiments were performed, *in situ*, in Jakolof Bay (Figure 1), where currents are significant due to an extremely high tidal range, the second greatest in North America at 9-10 m (Carroll 1994). Jakolof Bay has a relatively flat topographic profile (Feder and Jewett 1981, Carroll 1994), with a substrate composed predominantly of medium sand to cobble/rock (personal observations). Because *Pycnopodia helianthoides* were ubiquitous throughout the area, sites for these experiments were selected based on similarities in substrate and current regime. To ensure adequate current flow, experiments were performed at least 1.5 hours before or after slack tides. To ensure that seastars were actively foraging, choice experiments were performed during the summer (June through September 2001 and 2002), when seastars are most actively feeding (Jangoux 1982). For each experiment, the current direction and speed were determined *in situ* by ejecting 1 ml of lactose from a capillary tube and measuring the

time needed to travel one meter. The prey item used in these experiments was *Saxidomus giganteus* (the butter clam), a locally abundant bivalve normally consumed by *P. helianthoides* (Mauzey *et al* 1968). *Saxidomus giganteus* were collected intertidally in Jakolof Bay and kept in a continuous-flow seawater tank at the laboratory until they were used in experiments, but in no case were individuals held for more than 3 days. At the conclusion of each experiment, *P. helianthoides* were marked by clipping a small portion of one of the two arms located closest to the madreporite. *Pycnopodia helianthoides* found with clipped, damaged, or missing arms were not used in any experiment to prevent pseudoreplication.

Y-maze. To determine if *Pycnopodia helianthoides* use chemoreception to pursue introduced prey cues, a Y-maze (as described by Dale 1997) was designed to offer seastars a choice between experimental and control treatments. Forty replicate tests were performed between June and September 2001. The Y-maze was constructed using two rectangular plastic bins, that were open at both ends, measuring 0.45 m x 0.30 m x 0.25 m and fastened side to side using rubber straps (Figure 2a). A plexi-glass divider was placed between the plastic bins to separate the two sides of the Y-maze. The divider extended 20 cm beyond the ends of the plastic bins in the direction of the seastar. In order to ensure laminar flow, several thousand 12 cm plastic drinking straws were bundled together and arranged within the down-current end of the plastic bin.

Forty individual *Pycnopodia helianthoides* were tested for each of three clam manipulations: (1) a damaged clam vs. a shell control, (2) a live clam vs. a shell control and (3) a Y-maze control (no clams or shell controls on either side of the Y-maze). Experimental and control treatments were placed in randomly determined sides of the Y-maze. Damaged clams were broken open with a lead weight to ensure tissue damage just before timing began. Shell controls were empty clam shells collected in the local area that were broken with a lead weight to control for prey shape and other possible abiotic factors associated with breaking a clam shell. Based on pilot studies, live clams used in the Y-maze experiments were allowed to sit for 3 minutes so that they would begin processing water.

Before testing, the current speed and direction at the site were confirmed and the Y-maze was placed up-current of the *Pycnopodia helianthoides* with approximately 10 cm separating the end of the plexi-glass divider and the closest arm of the seastar. This was done to ensure the seastar being tested would receive flow from both sides of the Y-maze. Timing started with the introduction of the experimental and control treatments. In the experiments involving live clams, timing started at the end of the 3-minute processing period. Data taken included the time to detect, time to move, time to travel 20 cm to either side of the Y-maze, and the side, if any, of the Y-maze chosen. Arm curling and tube feet extension were used as indicators of chemosensory detection, as described for the “orienting response” discussed by Valentincic (1983). The time to move was noted as the time for a seastar to begin to move from its original position, as described for the “appetitive behavior” discussed by Valentincic (1983). The tests were concluded when a seastar reached either side of the Y-maze or 15 minutes had elapsed.

The results (experiment, control, or neither chosen) from each of the three treatments were analyzed with a one-way ANOVA, using Tukey’s post hoc test and SAS statistical software (Delwiche and Slaughter 1996).

Cue propagation. To determine the role of current flow in propagating cues, experiments were performed to observe the movement of seastars in 5 m² plots with a centrally located prey cue. Six replicates of this experiment were conducted between August and September 2001. In each replicate, an experimental and a control plot (a minimum of 10 meters apart) were marked using anchor weights and line. Circular Dungeness crab pots (1 m in diameter) were placed in the center of each of the plots to provide protected areas where fish or other scavengers could not disturb the prey cues (Figure 2b). To allow *P. helianthoides* that may have been disturbed during the set-up of the plots to recover, areas were marked during the morning tide and the experiments were performed during the evening tide. Each plot (experimental and control) was divided into two areas: down-current (45 degrees to each side of the center of the plot adjacent to the determined current direction) and up-current (the remaining 270 degrees of each plot) (Figure 2b).

Prey cues for experimental plots were six damaged *Saxidomus giganteus* placed in two perforated plastic bait boxes. The number of *S. giganteus* used was based on the mean density of clams found in the local intertidal by haphazardly sampling twenty 0.25 m² quadrats. Controls consisted of six damaged *S. giganteus* shells in similar bait boxes. The plot receiving the prey cue was determined by a coin toss.

Red flags were placed beside each *Pycnopodia helianthoides* in the experimental and control plots prior to prey cue and control introductions. Flags were placed a few centimeters to the left of each *P. helianthoides* so as not to impede movement. To observe the path of individual *P. helianthoides* after prey cues and controls were introduced, multi-colored flags were placed next to each *P. helianthoides* at 5, 10, 20, 30, and 60-minute intervals. After the 60-minute marking, the distances and azimuths from each flag to the center of the crab-pot were measured.

Each replicate of this experiment was a minimum of 15 m up-current of the previous trial, to prevent testing seastars that may have already detected the prey cue. Because each plot (experimental and control) for each of the replicates had a different number of *Pycnopodia helianthoides*, activities (moving and reaching the prey cues) were reported as percent of the total seastars for that plot performing the activity.

A two-way ANOVA (location and treatment), using a Tukey post hoc and SAS, was performed to compare the mean percent of seastars that moved to the prey cue, and the mean percent of seastars that reached the prey cue.

Corridor. To determine if *Pycnopodia helianthoides* would bypass live prey to reach damaged prey, a corridor cage (Figure 2c) was constructed using PVC pipes (1 m x 0.8 m x 0.5 m) to direct *P. helianthoides* through an area where a live clam was located down-current of a damaged clam. Wood slats were attached to the two vertical sides of the PVC cage to reduce outside influences while lead weights and rebar were used to weight the corridor.

Corridor experiments were conducted from June to September 2002. The corridor was oriented parallel to the current flow and placed up-current of the seastar being tested. Each *Pycnopodia helianthoides* was offered one of four treatments: (1) a damaged

Saxidomus giganteus up-current of a live undamaged *S. giganteus*, (2) a damaged *S. giganteus* up-current of a live *S. giganteus* when *P. helianthoides* were found in excavations, (3) only a damaged *S. giganteus* and (4) only a live *S. giganteus*. Each treatment was replicated 15 times using different seastars. Live clams were placed 10 cm up-current of the *P. helianthoides* being tested, buried siphon-side up so the top of the clam was even with the surface of the substrate, and were allowed 3 minutes to begin processing water before the introduction of the damaged clam. Damaged clams were broken with a lead weight and placed on the seafloor one meter up-current of the live clams. Experiments were concluded when *P. helianthoides* either reached the damaged clam, stopped at the live clam or 15 minutes elapsed. Divers recorded the time for each of the end results (damaged clam, live clam, or neither).

SAS statistical software was used to analyze the results (damaged clam, live clam, or neither) from each of the four treatments in the corridor experiment. A one-way ANOVA with a Tukey post hoc was performed to test for significant differences between the results of the treatments (Delwiche and Slaughter 1996).

Supplemental food experiment (Short-term effects)

To determine if *Pycnopodia helianthoides* would change foraging modes from predator to scavenger when scavengable prey was introduced, a supplemental food experiment was performed from June to September 2002. For this, six sites were selected based upon similarities in substrate type (sand), current flow dynamics (0.1 to 0.01 m/s), and the presence of *P. helianthoides* and bivalve species *Saxidomus giganteus* and *Prototheca staminea* (for site locations see Figure 1). Experimental and control sites (20 m radius circles) were established randomly but were grouped in pairs so that local conditions would be similar. The distance between experimental and control sites was at least 500 m to ensure independence and to avoid edge effects. One site group had a high-density of *P. helianthoides* (50-80 in each 20m radius circle), another group had a medium-density of *P. helianthoides* (5-45 in each 20m radius circle), and the last group had low-densities of *P. helianthoides* (0-5 in each 20m radius circle).

At each of the sites, four concentric circles within the 20 m radius circles were marked to observe *Pycnopodia helianthoides* distributions over a 4-week period (Figure 3). The concentric circles, with radii of 20, 15, 10, and 5 m, were marked using multi-colored flagging tape tied to 6-inch long wire hoops pushed into the substrate. The interval of radii of the concentric circles was kept consistent to facilitate the observation of movement towards the center of the site. Air-filled capillary tubes were attached to the end of each of the flags to keep them buoyant and upright. Prior to experimentation, *P. helianthoides* densities and distributions were established in each of the circles.

Before sampling, bivalve densities were estimated at a distance between 25 and 35 m from the center point at each site in fifteen 0.25 m² quadrats using a venturi suction dredge. To ensure no edge effects, a 5 m buffer zone was established between the dredges performed pre-experimental (outside) and post-experimental (inside) each of the sites. Power analysis was performed on the dredges performed outside each site to determine the minimum number of dredges necessary to obtain an accurate estimate of the bivalve population inside each site while minimizing destructive sampling (Zar 1999). As a result, thirty 0.25 m² quadrats per site were sampled before supplemental food was introduced, and then again after the 4 week experiment. To account for the patchy distribution of bivalves at each site, a stratified sampling technique was implemented to estimate the bivalve population. Sites were dredged in random order to ensure there were no time/efficiency biases.

After initial quantification of seastar and bivalve densities at each of the sites, six decomposing halibut carcasses were placed in the center of each experimental site every 4 days for 4 weeks. Halibut carcasses were used in lieu of *Saxidomus giganteus* to minimize the destruction of bivalve resources while maintaining a large cue surface area. The halibut were recently caught and cleaned, and were obtained from the Seldovia dock "gurry bin," a fish waste collection area. The corresponding control sites did not receive halibut carcasses. In preliminary experiments, *Pycnopodia helianthoides* reacted equally to cues released by clams and fish. Experimental and control sites were observed initially, for five consecutive days, and then every 2 to 3 days thereafter. To determine

changes in *P. helianthoides* distributions, densities of *P. helianthoides* were measured in each circle as a percentage of the total found at that site. The foraging activities of *P. helianthoides* were noted as a percentage of the total number of seastars observed in excavations. To determine if the total number of excavations found within each of the sites changed over time, divers counted the number of excavations encountered in each of the circles on each dive.

Since each of the three sites had different densities of *Pycnopodia helianthoides* initially and would therefore have different interaction effects, each site pair was considered as a separate experiment. Because these experiments were not replicated, statistical analyses could not be performed (Littell *et al* 1991, Stokes *et al* 2000). General trends and obvious relationships will be discussed.

Supplementation survey (Long term effects)

To determine if local populations of *Pycnopodia helianthoides* located in areas where scavengable prey is readily available had adopted a full-time scavenging mode, comparisons were made between two populations of *P. helianthoides*, one in the presence of seasonally available prey and the other without. From 16 to 24 August 2002, observations were made under Jakolof dock, where local fishermen discard fish carcasses, damaged/cleaned shellfish and other organic refuse. As a control, an adjacent but uninfluenced area (approximately 600 m away) within the same embayment, with similar depth, substrate, and current characteristics, was observed (Figure 1).

For these surveys, divers quantified the density and activity of *Pycnopodia helianthoides* located within a 600 m² area directly under Jakolof dock and at the adjacent site. The sites were observed every other day for 10 days to determine if there were any short-term temporal differences in the densities or activities of the *P. helianthoides* populations. Upon completion of these observations, divers dredged thirty 0.25 m² quadrats to determine local clam densities.

The density of *Pycnopodia helianthoides* and the percent of *P. helianthoides* in excavations at each site were analyzed using a repeated measures ANOVA. The

differences in clam densities at the two sites were analyzed using a t-test with STATISTICA.

RESULTS

General

In the experiments described below, *Pycnopodia helianthoides* densities ranged from $0.5/\text{m}^2$ to $0/\text{m}^2$ with an average of $0.022 \pm 0.005 \text{ SE}/\text{m}^2$. *Pycnopodia helianthoides* size (arm tip to arm tip) averaged $52 \pm 1 \text{ SE cm}$ ($n = 594$). *Saxidomus giganteus* average weight was $0.13 \pm 0.006 \text{ SE kg}$ and measured $13.3 \pm 0.6 \text{ SE cm}$ ($n = 176$) across. The mean current speed observed in Jakolof Bay was $0.04 \pm 0.001 \text{ m/s}$.

Choice experiments

Y-maze. *Pycnopodia helianthoides* showed a significantly greater response to damaged clams than live clams, shell controls and Y-maze controls in the Y-maze experiments (Figure 4, ANOVA, $F = 72.54$, $P < 0.0001$, $n = 40$). Responses to live clams and Y-maze controls were not significantly different from each other (ANOVA, $F = 1.30$, $P = 0.259$, $n = 40$).

When given a choice between a damaged clam and a shell control, 83% of the 40 *Pycnopodia helianthoides* tested chose the damaged clam side of the Y-maze, 2% chose the shell control side and 15% failed to reach either side (Figure 4). The mean times to detect, move, and reach the Y-maze can be found in Table 1. When given a choice between a live clam and a shell control, 5% of the 40 *P. helianthoides* tested chose the live clam side of the Y-maze, 5% chose the shell control side of the Y-maze, and 90% did not respond to either side (Table 1, Figure 4). When 40 *P. helianthoides* were tested using the Y-maze without any experimental cues, 3% moved to the left side of the Y-maze, 5% moved to the right side of the Y-maze, and 92% did not move to either side (Table 1, Figure 4).

Cue propagation. *Pycnopodia helianthoides* located in the experimental down-current areas moved to (ANOVA, $F = 18.12$, $P = 0.0004$, $n = 6$) and reached (ANOVA, $F = 15.94$, $P = 0.0007$, $n = 6$) the prey cue significantly more than the *P. helianthoides* located in the experimental up-current, control down-current, and control up-current areas (Figure 5, Table 2). *Pycnopodia helianthoides* located in experimental up-current,

control down-current and control up-current areas did not differ significantly from each other in seastars moving to (ANOVA, $F = 0.05$, $P = 0.953$, $n = 6$) or reaching (ANOVA, $F < 0.0001$, $P = 0.9999$, $n = 6$) the prey cue or cue control.

The mean percent of *Pycnopodia helianthoides* that moved to the prey cue from the experimental down-current areas ($83\% \pm 17$ SE) was greater than the mean percent that moved to the prey cue from the experimental up-current areas ($6\% \pm 4$ SE), the control down-current areas ($4\% \pm 4$ SE), and control up-current areas ($6\% \pm 6$ SE) (Figure 5). The mean percent of *P. helianthoides* that reached the prey cue from the experimental down-current areas ($72\% \pm 18$ SE) was greater than the mean percent that reached prey cue from the experimental up-current areas ($0\% \pm 0$ SE), the control down-current areas ($0\% \pm 0$ SE), and the control up-current areas ($0\% \pm 0$ SE) (Figure 5).

The mean distance *Pycnopodia helianthoides* traveled to reach the prey cue was 1.8 ± 0.2 SE meters ($n = 10$ seastars), with seastars moving from 1.2 m to 2.5 m. The initial distance of the seastars to the cue did not affect the result. The mean movement rate for seastars that reached the prey cue was $11.9 \text{ m/h} \pm 2.2$ SE, with a range of 3.8 to 27.6 m/h. One seastar entered the plot 10 minutes after timing began and traveled 2.23 m to the prey cue, so it came from a longer distance than measured.

Corridor. Similar to the Y-maze experiments, *Pycnopodia helianthoides* showed a significantly greater response to damaged *Saxidomus giganteus* than live *S. giganteus* in the corridor experiments. Each of the treatments where damaged *S. giganteus* were offered to *P. helianthoides* up-current of live *S. giganteus* resulted in significantly more seastars instigating a foraging response than in the treatment without damaged *S. giganteus* (Figure 6, Table 3, ANOVA, $F = 62.52$, $P < 0.0001$, $n = 15$). Each of the three treatments that included the use of damaged *S. giganteus*, were not significantly different from one another (ANOVA, $F = 0.09$, $P = 0.9152$, $n = 15$).

When a damaged *Saxidomus giganteus* was placed up-current of a live *S. giganteus*, 13 of the 15 *Pycnopodia helianthoides* tested moved past the live *S. giganteus* to get to the damaged *S. giganteus* (Figure 6). Of the two *P. helianthoides* that did not reach the damaged *S. giganteus*, one seastar stopped at the live *S. giganteus* and the other

failed to move from its original position. Of the *P. helianthoides* found in excavations, 13 of 15 left the excavations and then moved past the live *S. giganteus* to get to the damaged *S. giganteus*. Of the two seastars in excavations that did not reach the damaged *S. giganteus*, one stopped at the live *S. giganteus* and the other did not move from its original position. When *P. helianthoides* were offered only damaged *S. giganteus* in the corridor, 14 out of 15 seastars reached the damaged *S. giganteus*, the remaining one did not move from its original position. In the treatment in which *P. helianthoides* were offered only live *S. giganteus*, none of the 15 seastars reacted within the 15-minute time period (Figure 6).

Supplemental food experiment

Food provided to local populations of *Pycnopodia helianthoides* altered community structure in some cases. The distribution and foraging activities of *P. helianthoides* changed when scavengable prey was introduced. This change in foraging modes had measurable effects on the bivalve prey populations that *P. helianthoides* is normally found to eat.

Seastar distributions. Initially, 35% of 56 *Pycnopodia helianthoides* found at the high-density experimental site were located within the 5 m radius circle. After the carcasses were added, the distribution of *P. helianthoides* in the 5 m circle increased to a mean of 65% of 76 ± 5 SE seastars over the following 4-weeks (Figure 7a). The percentage of *P. helianthoides* in the larger circles of the high-density experimental site varied between 10 and 30%. The percentage of *P. helianthoides* in the circles of the high-density control site (72 ± 3 SE seastars) all varied between 10 and 50% (Figure 7a).

Initially, none of the 6 *Pycnopodia helianthoides* found at the medium-density experimental site were located within the 5 m circle (Figure 7b). After the fish remains were added, the distribution of *P. helianthoides* in the 5 m circle increased to a mean of 63% of 10 ± 1 SE seastars for the length of the experiment (Figure 7b). The percentage of *P. helianthoides* in the other circles of the medium-density experimental site varied

between 0 and 40%. The distribution of *P. helianthoides* in the circles of the medium-density control site (25 ± 2 SE seastars) all varied between 0 and 40% (Figure 7b).

The percentage of *Pycnopodia helianthoides* located within the 5 m circle of the low-density experimental site did not change when food was added (Figure 7c). There were no obvious differences in the distributions of the few *P. helianthoides* located within any of the circles of the low-density experimental or control sites (Figure 7c).

Foraging activities. At the high-density sites, the mean percentage of *Pycnopodia helianthoides* digging in the control site was $45\% \pm 3$ SE, compared to $20\% \pm 3$ SE at the experimental site (Figure 8). The mean percentage of *P. helianthoides* digging at the medium-density control site was $27\% \pm 4$ SE, compared to $2\% \pm 2$ SE at the corresponding experimental site (Figure 8). No seastars were observed excavating at either of the low-density sites. The number of excavations observed in the experimental and control sites did not appear to change over time at the high-density, medium-density, or low-density sites (Figure 9). Although excavations were not monitored to determine the recovery rate, the general trend in the numbers of excavations at the high-density and medium-density sites showed that the number of excavations decreased over time in the experimental areas and remained the same or increased in the control areas. The variance in the number of excavations observed was largely due poor water clarity. Also, problems in determining what constituted an excavation may have been a source of error.

Prey densities. When comparing the clam densities pre-experimentation and post-experimentation at each of the experimental sites, only the medium-density site showed a significant change in clam density (Figure 10, ANOVA, $F = 51.50$, $P < 0.0001$, $n = 30$ quadrats). The density of clams at the high-density experimental site increased from 1.1 ± 0.2 SE to 1.9 ± 0.3 SE clams/ 0.25 m^2 (Figure 10). The density of clams at the medium-density experimental site increased from 1 ± 0.3 SE to 7.7 ± 0.9 SE clams/ 0.25 m^2 (Figure 10). The density of clams at the low-density experimental site increased from 2.3 ± 0.4 SE to 3.4 ± 0.5 SE clams/ 0.25 m^2 (Figure 10). At the control sites, none had any significant changes in clam densities (Figure 10). The clam populations at the high-density, medium-density and low-density control sites changed from 1 ± 0.2 to 2 ± 0.4 SE

clams/0.25 m², 0.7 ± 0.2 to 0.7 ± 0.1 SE clams/0.25 m² and 1.1 ± 0.2 to 1.1 ± 0.2 SE clams/0.25 m², respectively (Figure 10, n = 30).

Supplementation survey

Clear differences were found between the populations of *Pycnopodia helianthoides* located at the dock site and the control site. The density of *P. helianthoides* at the dock site, where scavengable prey has been added for years, was significantly higher than the density of seastars at the control site, where no scavengable prey is known to have been added (0.28 ± 0.03 SE/m² vs. 0.025 ± 0.002 SE/m², Figure 11, repeated measures ANOVA, $F = 5.5$, $P = 0.02$). The percent of *P. helianthoides* in excavations at the control site was significantly higher than that at the dock site (46 ± 2.5 SE vs. 1.7 ± 0.4 SE, Figure 11, repeated measures ANOVA, $F = 160.8$, $P = 0.0062$). The dock site, which had an average of 165 ± 16 SE *P. helianthoides*, had only 12 excavations in the 600 m² area, while the control site that had an average of 15 ± 1 SE *P. helianthoides* and 26 excavations (n = 5 observations). The clam density at the dock site (1 ± 0.16 SE clams/0.25 m², n = 30), where *P. helianthoides* were so dense they were touching each other and scavengable prey have been discarded by boaters for years, was almost double that found at the control site (0.6 ± 0.16 SE clams/0.25 m², n = 30 quadrats). However, clam densities at the two sites were not statistically significantly different from each other due to high variances.

DISCUSSION

The results of the experiments and observations reported here support the hypothesis that *Pycnopodia helianthoides* is a facultative scavenger that depends on chemoreceptive abilities to locate damaged or decaying prey. This study also demonstrates that the foraging techniques used by this seastar will influence the role that it plays, and ultimately the effect that it has on the benthic community. While past studies on scavengers have focused on a particular time scale, be it immediate (< 1 hour) (Wobber 1975, Oliver *et al* 1985, Hall *et al* 1994, Evans *et al* 1996), short term (< 8 week) (Himmelman 1988, Veale *et al* 2000, Ross *et al* 2002), or long term (> 1 year) (McKillup and McKillup 1997), this study attempted to address all three time scales.

Pycnopodia helianthoides use chemoreception to actively pursue introduced damaged- or dead-prey cues. Scavengers, such as seastars, attracted by chemicals released by damaged tissues aggregate around injured prey items (Warner 1979, Kaiser and Spencer 1996, Veale *et al* 2000). Similar to studies on other scavengers, this study showed that *P. helianthoides* reacted to damaged bait more than to live bait (Zimmer-Faust and Case 1982, Miller 1990, Zhou and Shirley 1997). Damaged or dead organisms, including bivalves, fish, polychaetes, and echinoderms, are often the result of anthropogenic processes such as commercial fishing. Trawls and dredges that disturb the sediment damage or destroy many benthic organisms (Groenewold and Fonds 2000, McConnaughey *et al* 2000, Mensink *et al* 2000). A scavenger that is able to survive the passage of a beam trawl, or move into a disturbed area quickly, clearly has a competitive advantage because of the increased amount of food locally available (Kaiser and Spencer 1996). As with trawling, the practice of dumping fish waste selects for organisms that scavenge (Dayton *et al* 1995). *Pycnopodia helianthoides* has now been shown to have the ability to respond immediately to introduced damaged or dead prey cues, giving this seastar an advantage over slower or non-chemoreceptive organisms.

The chemical cues released when clams were damaged initiated a foraging response from *Pycnopodia helianthoides*, but the natural effluent from live clams did not.

This may be due to the dilution or diffusivity of the two types of cues. The chemical cues released from the damaged clam tissues provide a continuous source that seastars can follow. The natural effluent released from live clams may not be continuous or may be too dilute for the seastar to follow. The costs associated with locating suitable prey may be high, so it is energetically efficient for the seastar to search for continuous cues like damaged or decaying organisms, or contact cues such as a clam beds. This study also has shown that *P. helianthoides* will bypass live prey to reach damaged prey. *Pycnopodia helianthoides* found in excavations abandoned their quarry to search for damaged clams. This suggests that excavating is not always successful. Optimal foraging theory predicts that predators should go after prey that have a low search/handling time, low assimilation time and high energy content (Beddingfield and McClintock 1993, Hines *et al* 1997). The optimal scavenger should therefore be a generalist feeder that is mobile and sensitive to chemical cues.

In areas where current flow and tidal change are significant, scavengers that can chemically sense and move quickly are more likely to reach the source of the cue. Mobile predators having well-developed chemosensory abilities use water-borne signals to locate prey (Himmelman 1988). This study supports the theory that there is a direct relationship between ambient water currents and the arrival of scavengers (Himmelman 1988, Veale *et al* 2000). Though it was not possible to control for the amount of potential prey cue released by damaged clams or the level of damage done to each clam, both small (≈ 10 cm in length) and large (≈ 17 cm in length) injured clams instigated a foraging response.

This study demonstrated that *Pycnopodia helianthoides* located in areas where scavengable prey is introduced adopt a scavenging role in lieu of a predatory role. In experimental treatments of the supplemental food experiment, more seastars were found on the carcasses than in excavations for clams. The distribution of *P. helianthoides* populations observed in the inner 5 m radius circle of the high-density and medium-density experimental sites were most likely the result of the chemosensory ability demonstrated in the choice experiments. When scavengable prey was continuously

added to experimental areas, *P. helianthoides* maintained a scavenging mode over the 4-week period. In the supplementation survey, large densities of *P. helianthoides* were observed under Jakolof dock, where fish/shellfish discards and other types of refuse have been introduced seasonally for years. Utilization of the dock tends to be highest during the spring and summer months. Despite the seasonality of introductions, observations made of this population at the end of winter revealed similar densities and activities as in spring/summer. This suggests that the population of *P. helianthoides* located under Jakolof dock may be scavenging full-time. The large density of *P. helianthoides* associated with the dock may be the result of intense and long-term chemical cues drawing seastars from long distances. Clearly, scavengers such as *P. helianthoides*, benefit greatly from anthropogenically introduced carrion and discards (Evans *et al* 1996, Garthe *et al* 1996, McKillup and McKillup 1997, and Veale *et al* 2000). Discards are often larger food sources than are naturally available, especially for benthic organisms (Wassenberg and Hill 1987, Garthe *et al* 1996, Lindeboom and deGroot 1998). In the North Sea, a single passage of a beam trawl produced enough food for scavengers to last between one and three weeks (Groenewold and Fonds 2000).

The foraging techniques observed at the three experimental sites of the supplemental food experiment were different from each other, probably due to the density of *Pycnopodia helianthoides* located at each of the sites. The low percentage of *P. helianthoides* found excavating, as well as the low number of excavations observed in the high-density and medium-density experimental sites, suggest that *P. helianthoides* were getting food from the carcasses and abandoning their predatory lifestyle. The much larger percentage of *P. helianthoides* excavating for clams at the high-density and medium-density control sites support this interpretation. *Pycnopodia helianthoides* will often "bout" or fight over food if supplies are limited or seastar densities are high (Wobber 1975). In this study, at the high-density site, access to the carcasses seemed to be limited as up to 10 *P. helianthoides* were on the carcasses at one time, with several others close by. On several occasions, *P. helianthoides* not located on the carcasses appeared to be boutting with other seastars. At the medium-density experimental site, *P.*

helianthoides had unlimited access to the carcasses and consequently no bouting was observed. These results are similar to those of Wassenberg and Hill (1987) who found that when scavengable prey is introduced, crabs will congregate around a food source and then break off a piece of the food and move a short distance away to avoid conflicts with conspecifics and other competitors. At the low-density site, the few *P. helianthoides* that were observed were not near the carcasses. *Telmessus cheiragonus* (the helmet crab) did, however, appear on a number of occasions, clipping off pieces of carcasses. *Telmessus cheiragonus* were also observed in the local areas foraging on dead seastars. In Juneau, Alaska, decapod crabs, such as *Cancer magister*, may limit the distribution of *P. helianthoides* by preying upon the seastars (Shirley pers. comm.). Direct interactions between *T. cheiragonus* and *P. helianthoides* were not observed during the experiment. Thus, the failure of *P. helianthoides* to react to the introduced fish carcasses in the low-density site remains unexplained. The supplementation survey provided further evidence for *P. helianthoides* shifting to a scavenging role when there is an opportunity to do so. Of the large number of *P. helianthoides* located at the dock site, very few were excavating for clams, resulting in a small number of excavations. At the control site, where scavengable food was not available, *P. helianthoides* occurred in lower numbers but were actively excavating for clams.

When *Pycnopodia helianthoides* are scavenging and not consuming bivalves, it is likely that this release in predation pressure, however small, allows more bivalves to survive to larger size classes. In one case, the medium-density experimental site of the supplemental food experiment, the number of clams captured by the 2 mm sieve was 7-fold greater at the end of the 4-week experiment than at the beginning. Most of the bivalves observed at this site, in the post-experiment dredges, were just large enough not to fall through the sieve (est. 5 mm length), so juvenile clams not previously detected may have grown to a collectable size. The relief in predation pressure, caused by *P. helianthoides* scavenging, may have allowed for these smaller and potentially easier to reach (short siphons) bivalves to survive, although it seems unlikely that adult seastars approximately 50 cm in diameter would eat such tiny bivalves. Paul and Feder (1975),

however, suggest that *P. helianthoides* often prefer a large number of small organisms to a few large organisms. Ross *et al* (2002) found that seastar predation decreased the number of juvenile bivalves from 300 to 35/m² and abridged the ability of clams to reach larger size classes. Fukuyama and Oliver (1985) found that in the presence of seastars, very few bivalves were observed exceeding 2 cm. At the high-density experimental site, there was little change in the density of bivalves pre-experimentation and post-experimentation. This may be because not all of the *P. helianthoides* at this site had access to the carcasses. Many of the *P. helianthoides* that did not have access to the carcasses were observed excavating, some within the 5 m circle. At the low-density experimental site, the clam densities pre-experimentation and post-experimentation did not change over the length of the experiment. The density of clams at all three control sites did not change significantly. According to the feeding rate of *P. helianthoides* determined by Breen (1979), one *P. helianthoides* could remove 200 large clams or about 400 small clams in a year. Considering this feeding rate and the dense aggregations of *P. helianthoides* observed in this study, this predator can play a significant role in the removal of prey organisms. When predation pressure is reduced, clam survival should increase.

The availability of scavengable prey, especially if provided continuously, may lead to long term benefits for scavengers like *Pycnopodia helianthoides*, such as increased growth or reproductive rates (Barbeau *et al* 1998, Veale *et al* 2000). Carrion availability plays an important role in the growth and success of all scavengers (McKillup and McKillup 1997). In Alaska, 3.4×10^5 tons of fish waste are discharged offshore every year by catcher-processor vessels (Bluhm and Bechtel 2003). In Kodiak, Alaska, approximately 400 tons of waste/day have been generated and dumped in the ocean since the mid-1980s (Himelbloom and Stevens 1994). This large amount of discharge could have a significant effect on where and what large populations of facultative scavengers, such as *P. helianthoides*, are eating. Such a discharge could significantly affect food-web dynamics.

CONCLUSIONS

The major objective of this study was to observe the chemosensory abilities and foraging techniques of *Pycnopodia helianthoides* in the presence of scavengable prey and to determine what effects this might have on the community. The choice experiments and the supplemental food experiment demonstrated that *P. helianthoides* do have chemosensory abilities that affect where and how these seastars forage. The supplemental food experiment and supplementation survey demonstrated that the introduction of scavengable prey affects the distribution and densities of seastars, the foraging activity of seastars, and possibly the relative success of prey that those seastars are normally found to consume. Whether the introduction of scavengable prey is immediate, short-term, or long-term, this study has demonstrated that when scavengable prey is introduced, the role of *P. helianthoides* changes from predator to scavenger.

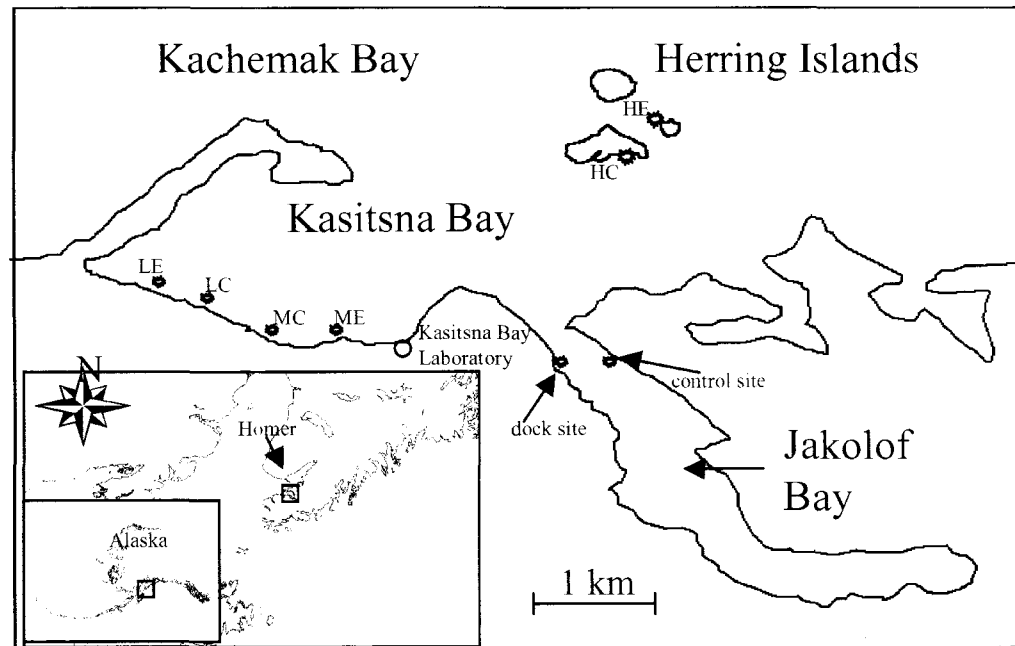


Figure 1. Location of Jakolof Bay and Kasitsna Bay Laboratory in southcentral Alaska. Sites are shown for the supplemental food experiment (LE = low-density experimental, LC = low-density control, ME = medium-density experimental, MC = medium-density control, HE = high-density experimental, HC = high-density control) and the supplementation survey (dock site and adjacent site).

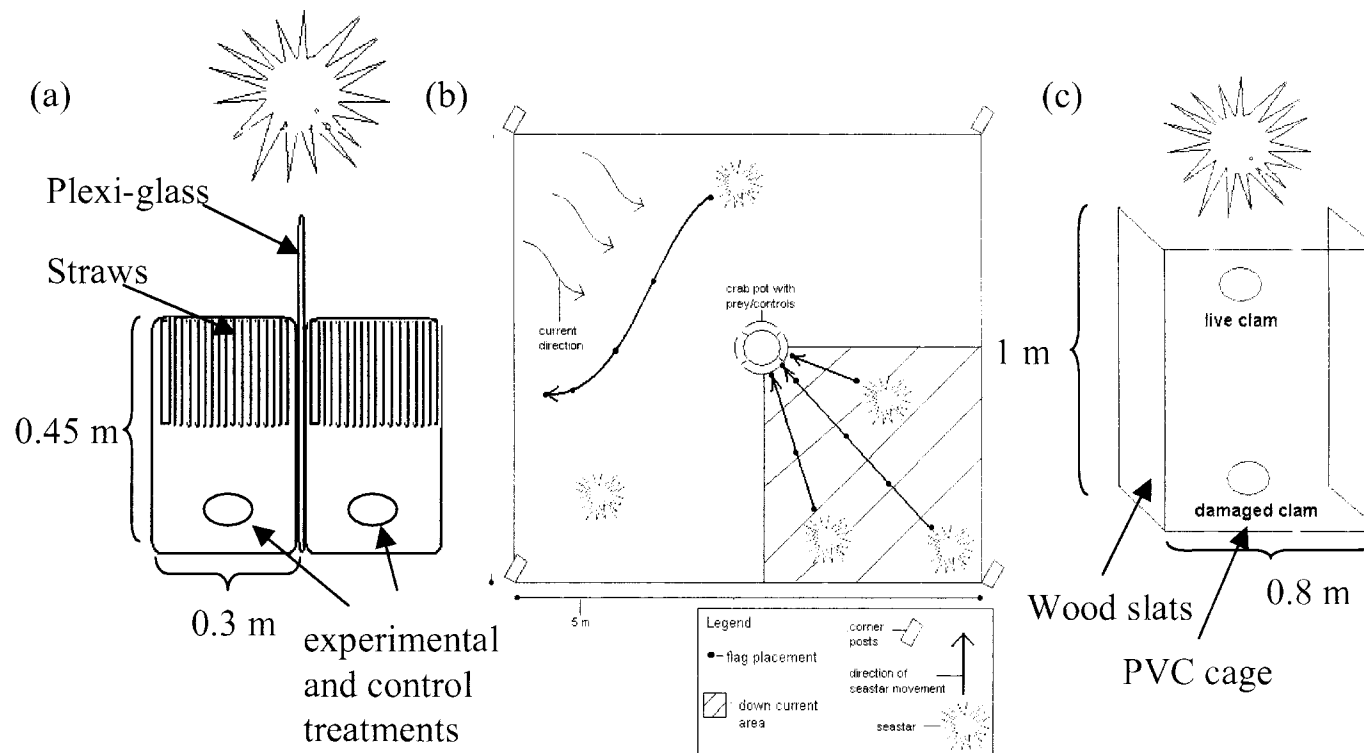


Figure 2. Diagram of (a) the Y-maze apparatus, (b) the cue propagation set-up, and (c) the corridor apparatus

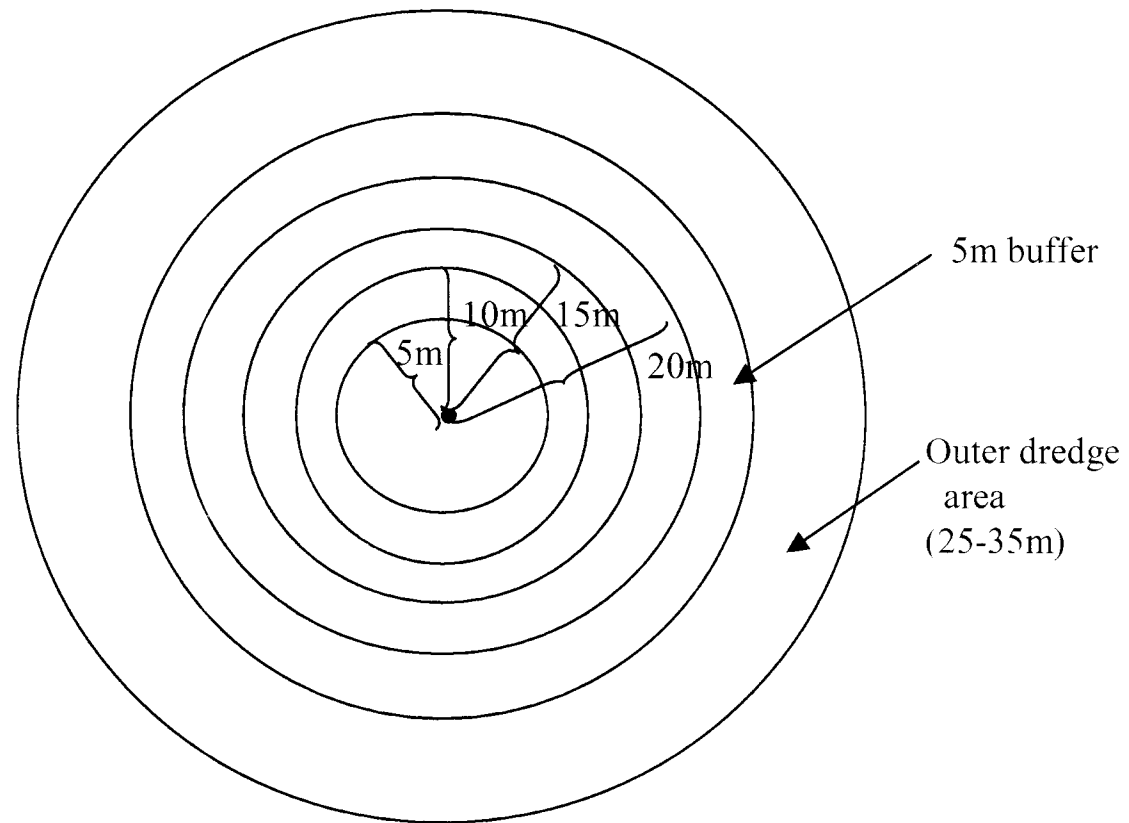


Figure 3. Diagram of concentric circles, and outer dredge area for the supplemental food experiment. (Circles were marked with grounding stakes and flagging tape)

Mean Number of *Pycnopoda heliarthroides*

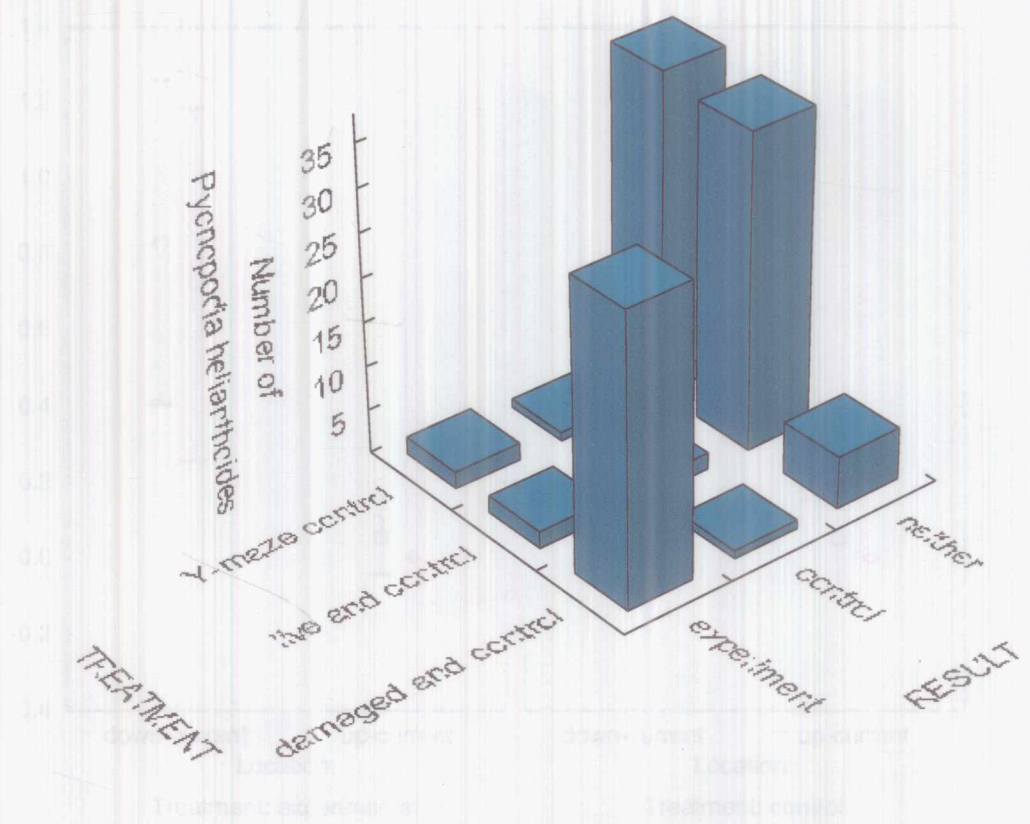


Figure 5. Mean number of *Pycnopoda heliarthroides* (n = 40/ treatment). Result refers to the direction that the seastar traveled. Treatment refers to the choice offered to each seastar. The Y-maze control was a choice between two broken clam shells. Each treatment is listed as experimental and control.

Figure 4. Y-maze experiments showing the treatments used and corresponding results (n = 40/ treatment). Result refers to the direction that the seastar traveled. Treatment refers to the choice offered to each seastar. The Y-maze control was a choice between two broken clam shells. Each treatment is listed as experimental and control.

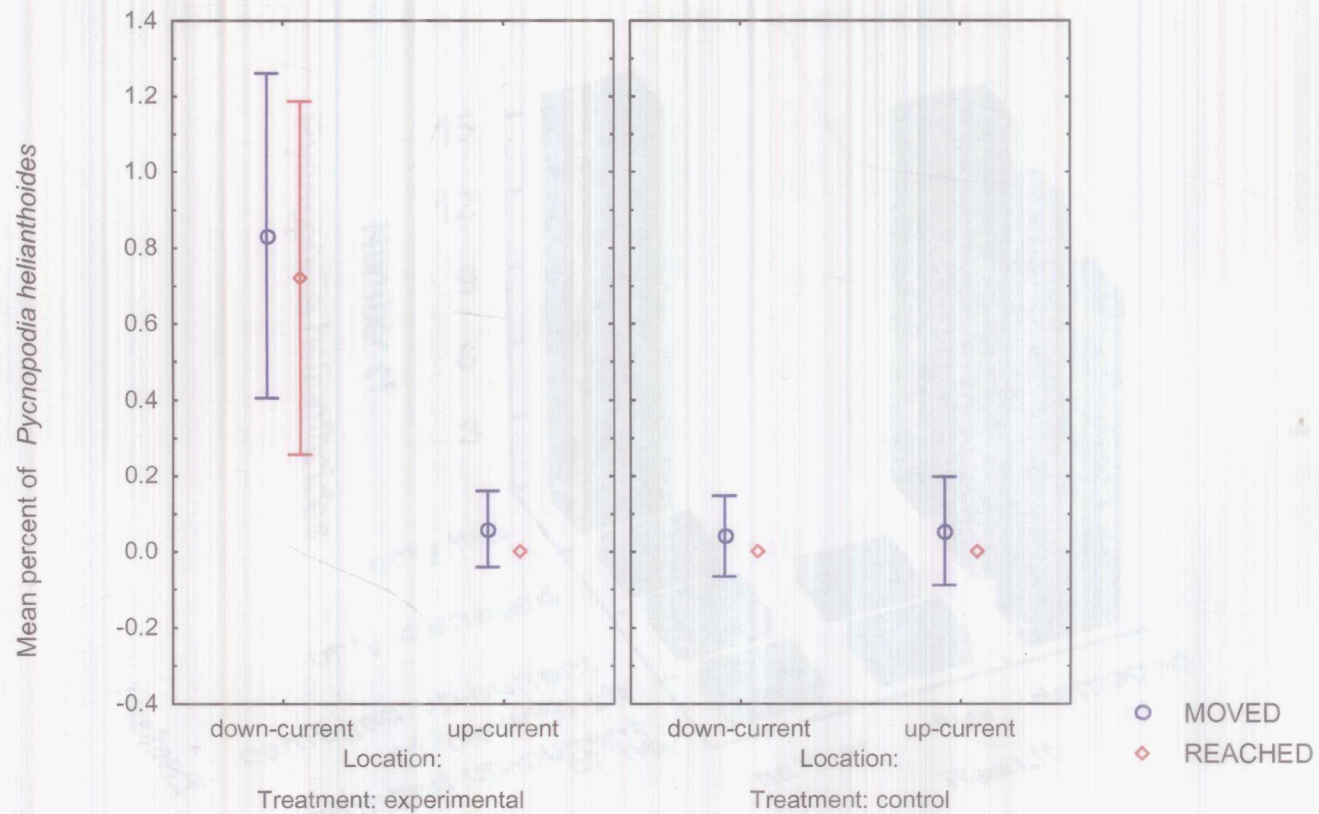


Figure 5. Mean percent of *Pycnopodia helianthoides* that moved (blue) and reached (red) the damaged *Saxidomus giganteus* offered in the cue propagation experiment. (\pm SE, n = 6/ treatment)

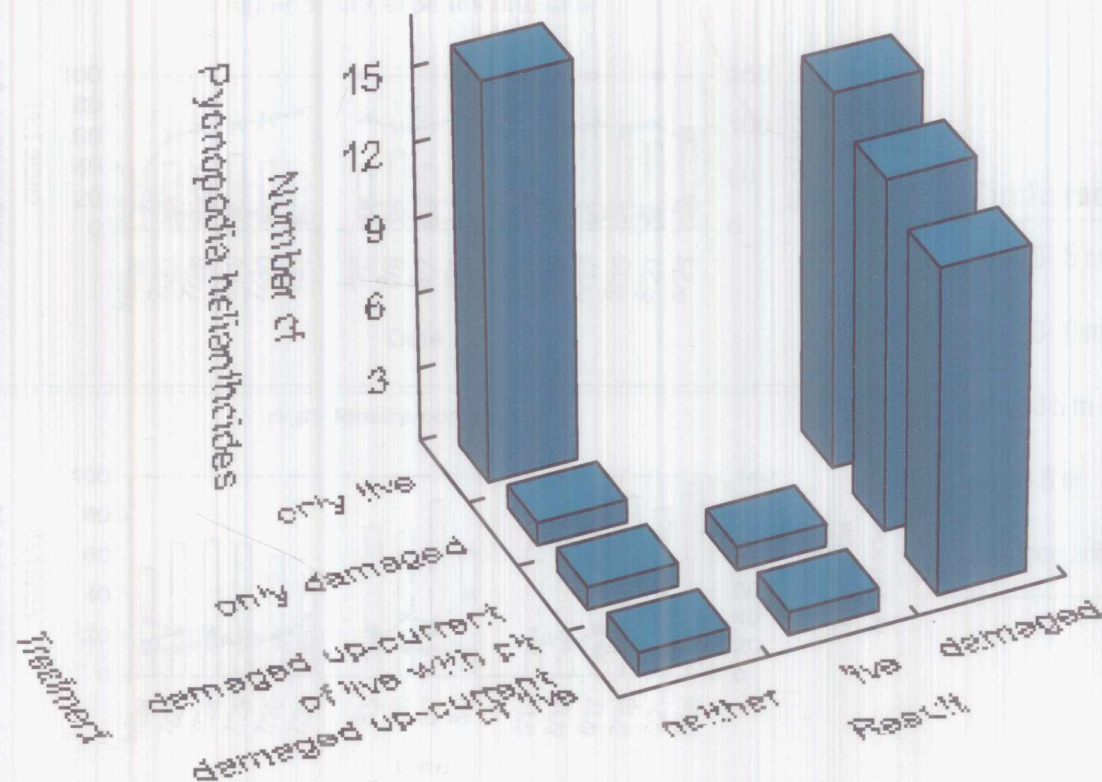


Figure 6. The corridor experiment showing the treatments and the corresponding results ($n = 15$ / treatment). The four treatments were damaged *Saxidomus giganteus* placed up-current of live *S. giganteus*, damaged *S. giganteus* up-current of live *S. giganteus* with *Pycnopodia helianthoides* found in excavations, only damaged *S. giganteus*, and only live *S. giganteus*.

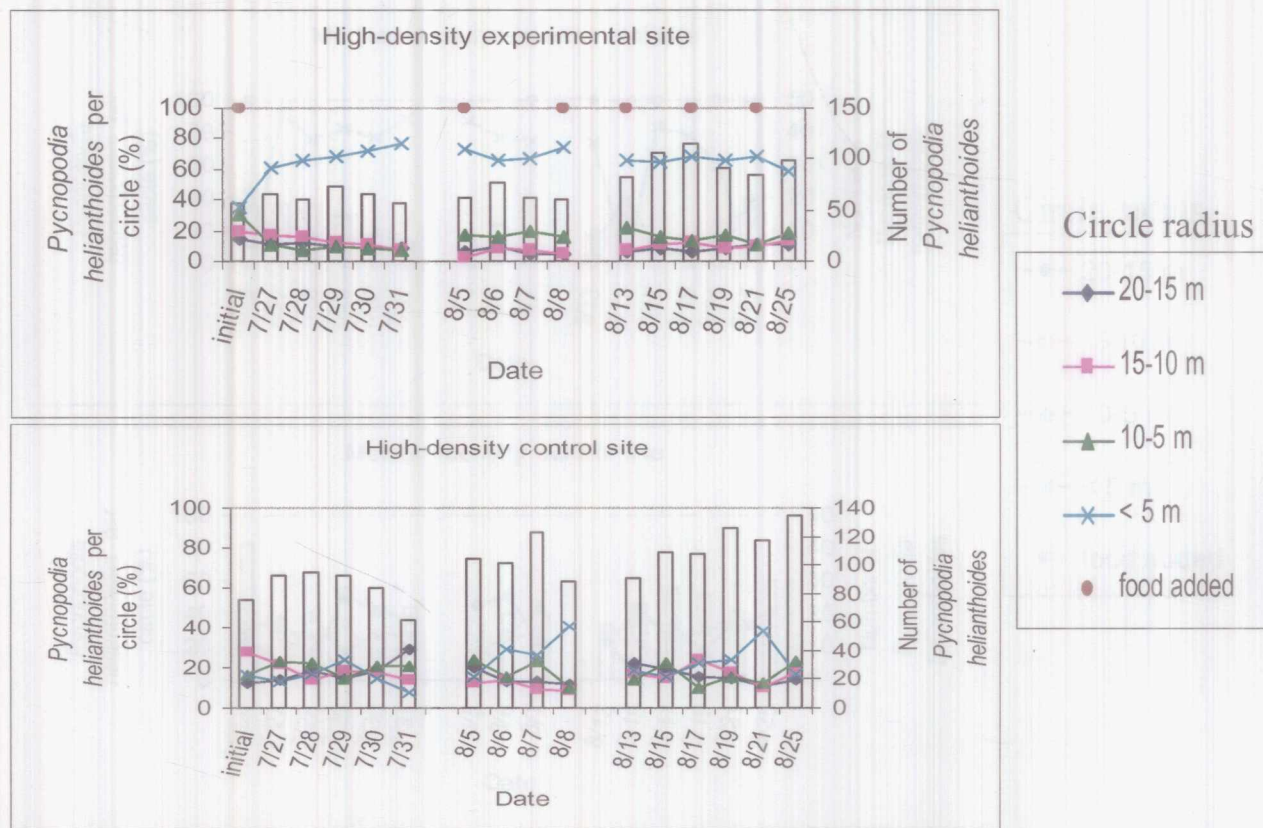


Figure 7a. Distribution of *Pycnopodia helianthoides* in each circle as a percentage of the total at the high-density sites during the supplemental food experiment. (Lines are percentages of *P. helianthoides* and bars are total numbers observed each measurement date)

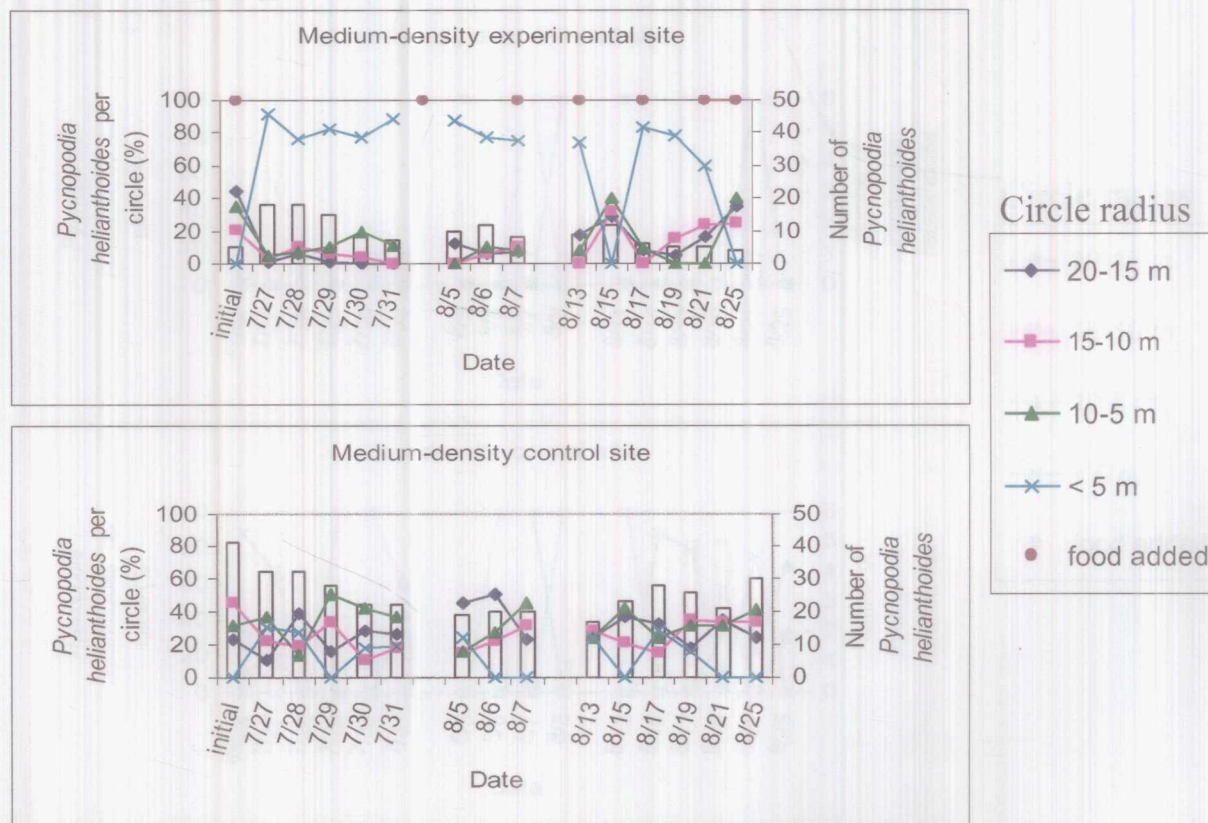


Figure 7b. Distribution of *Pycnopodia helianthoides* in each circle as a percentage of the total at the high-density sites during the supplemental food experiment. (Lines are percentages of *P. helianthoides* and bars are total numbers observed each measurement date)

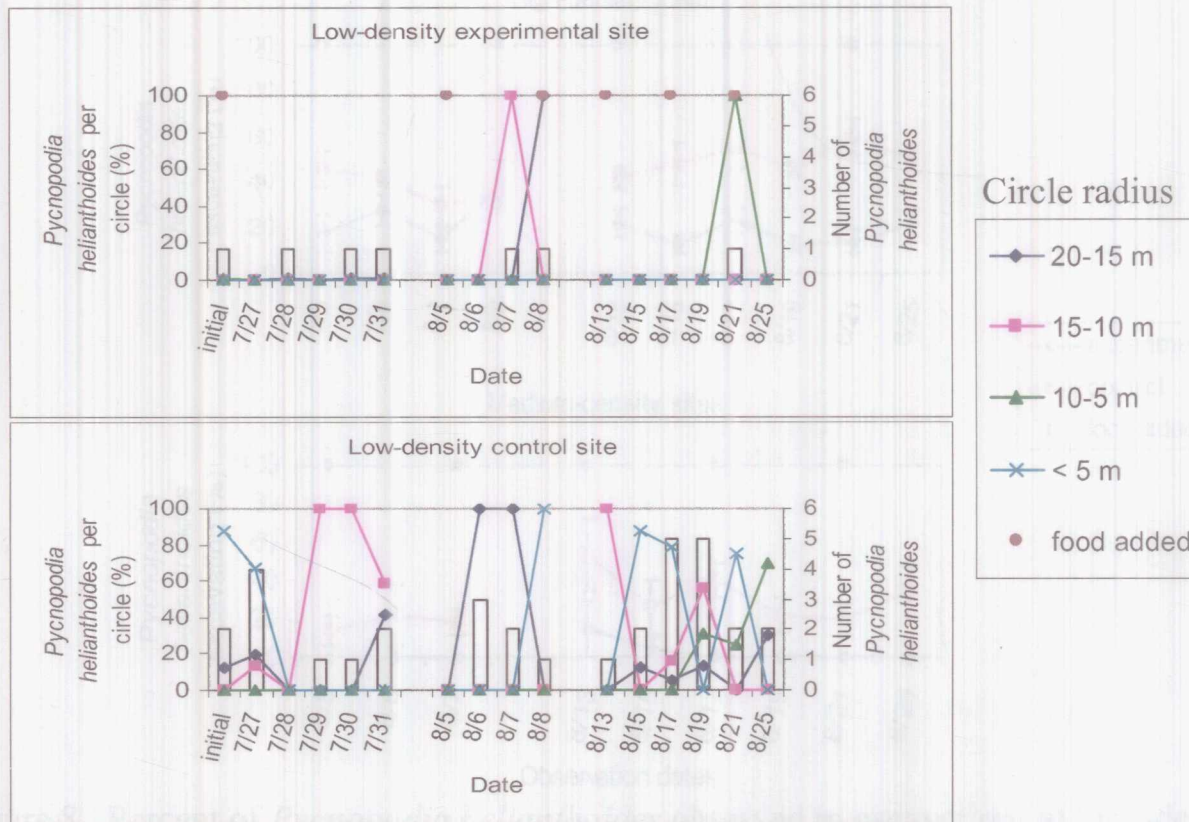


Figure 7c. Distribution of *Pycnopodia helianthoides* in each circle as a percentage of the total at the high-density sites during the supplemental food experiment. (Lines are percentages of *P. helianthoides* and bars are total numbers observed each measurement date)

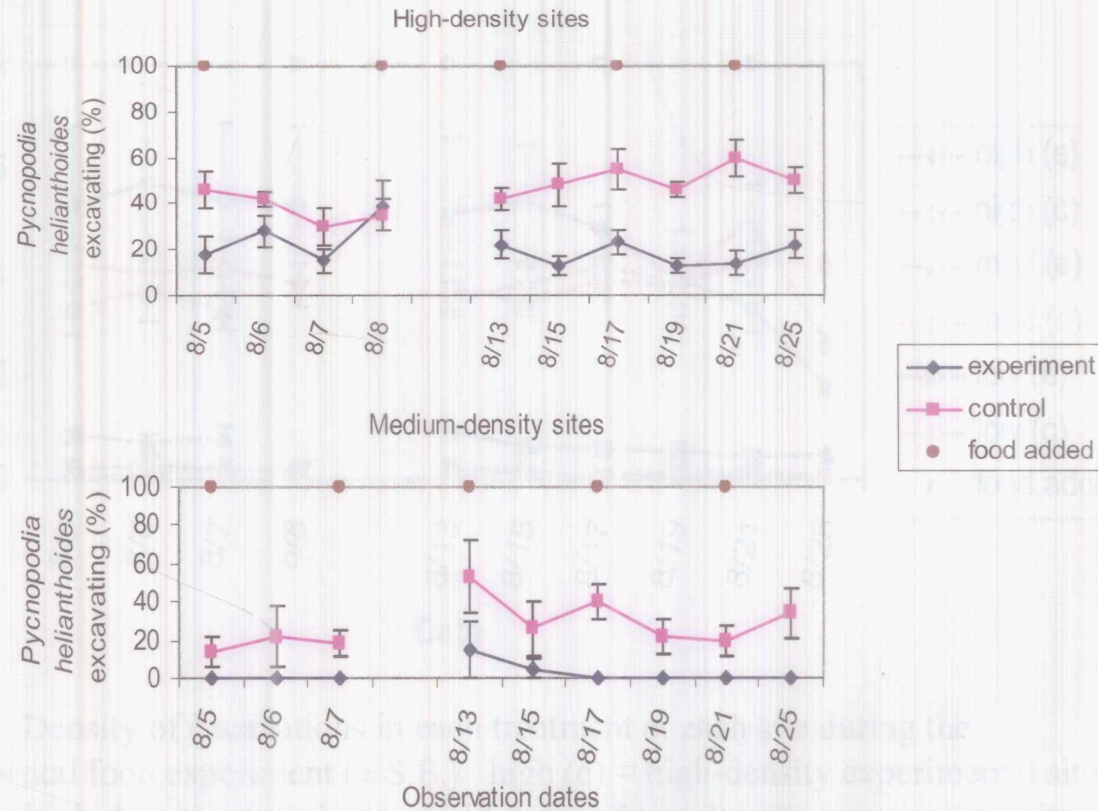


Figure 8. Percent of *Pycnopodia helianthoides* observed in excavations at high-density and medium-density sites during the supplemental food experiment (\pm SE). No seastars were observed digging excavations at the low-density site. (Dots are food additions and the break in data collection was due to logistical problems)

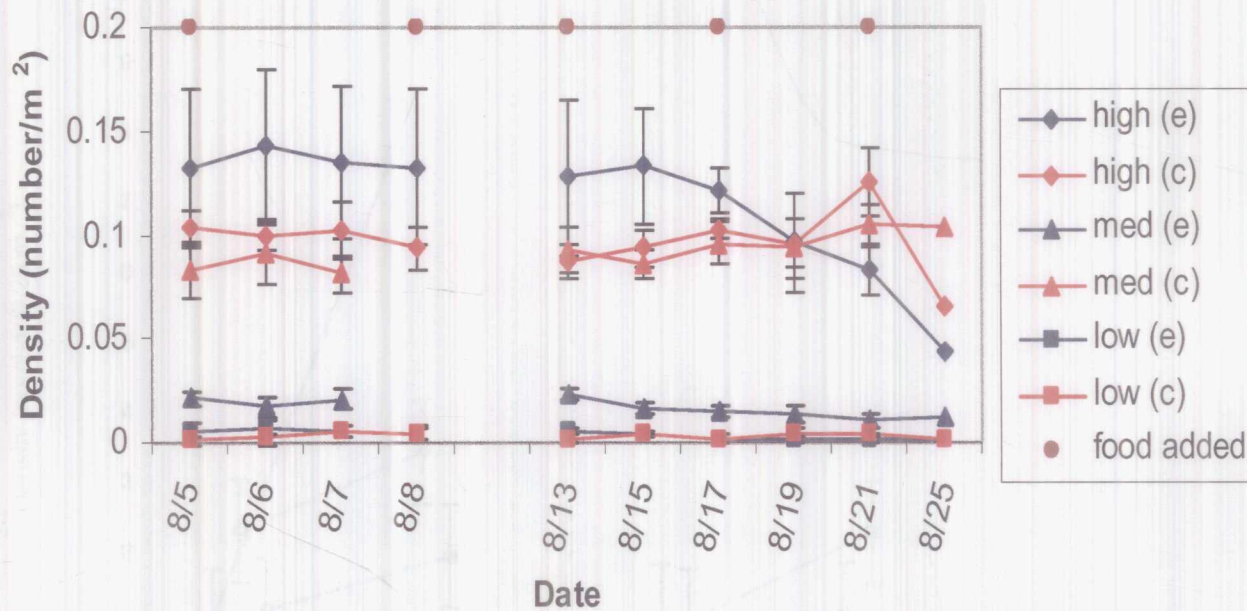


Figure 9. Density of excavations in each treatment at each site during the supplemental food experiment (\pm S.E.). high (e) = high-density experimental site, high (c) = high-density control site, med (e) = medium-density experimental site, med (c) = medium-density control site, low (e) = low-density experimental site, and low (c) = low-density control site. (Dots are food additions and the break between 8/8 and 8/13 was due to logistical problems)

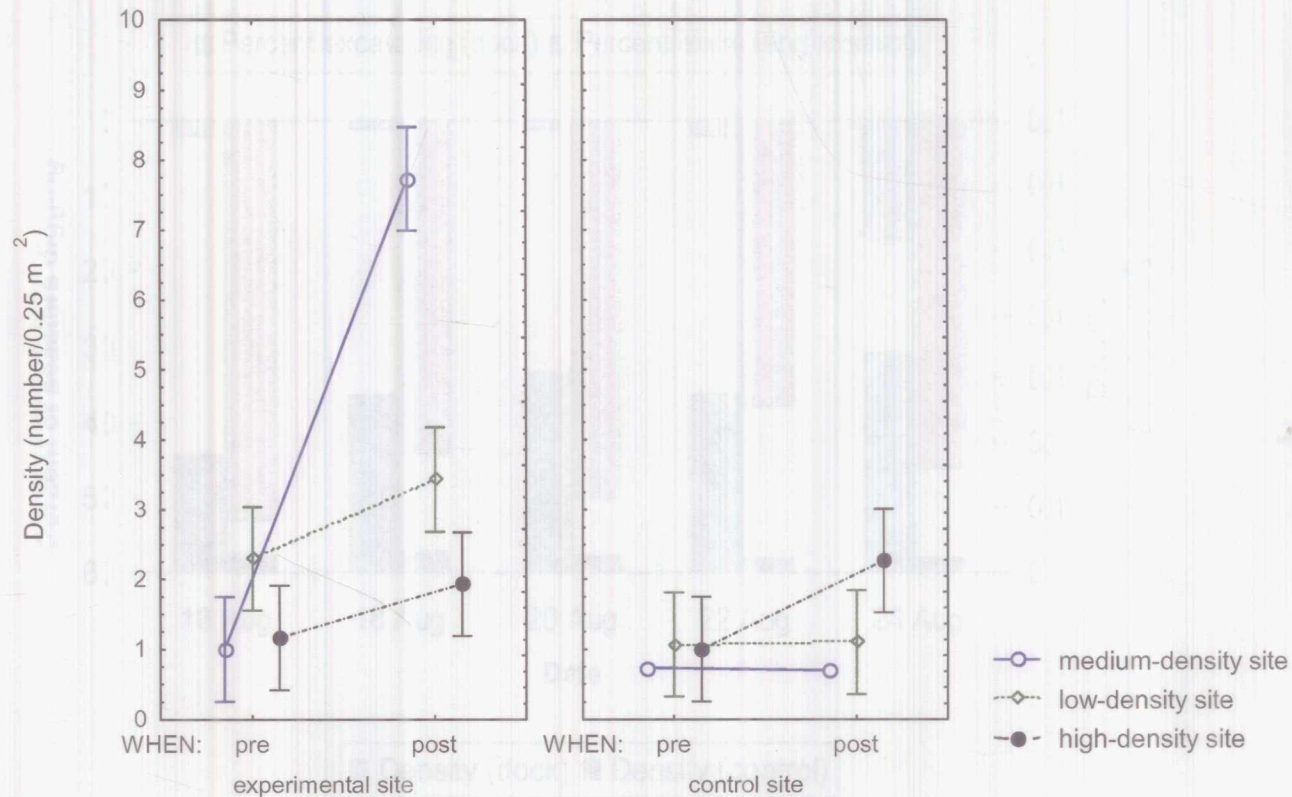


Figure 10. Mean clam densities (\pm S.E.) at each of the sites observed pre-experimentation and 4-weeks later (post experimentation) during the supplemental food experiment. (There were $n = 30$ quadrats pre and post for each treatment and density)

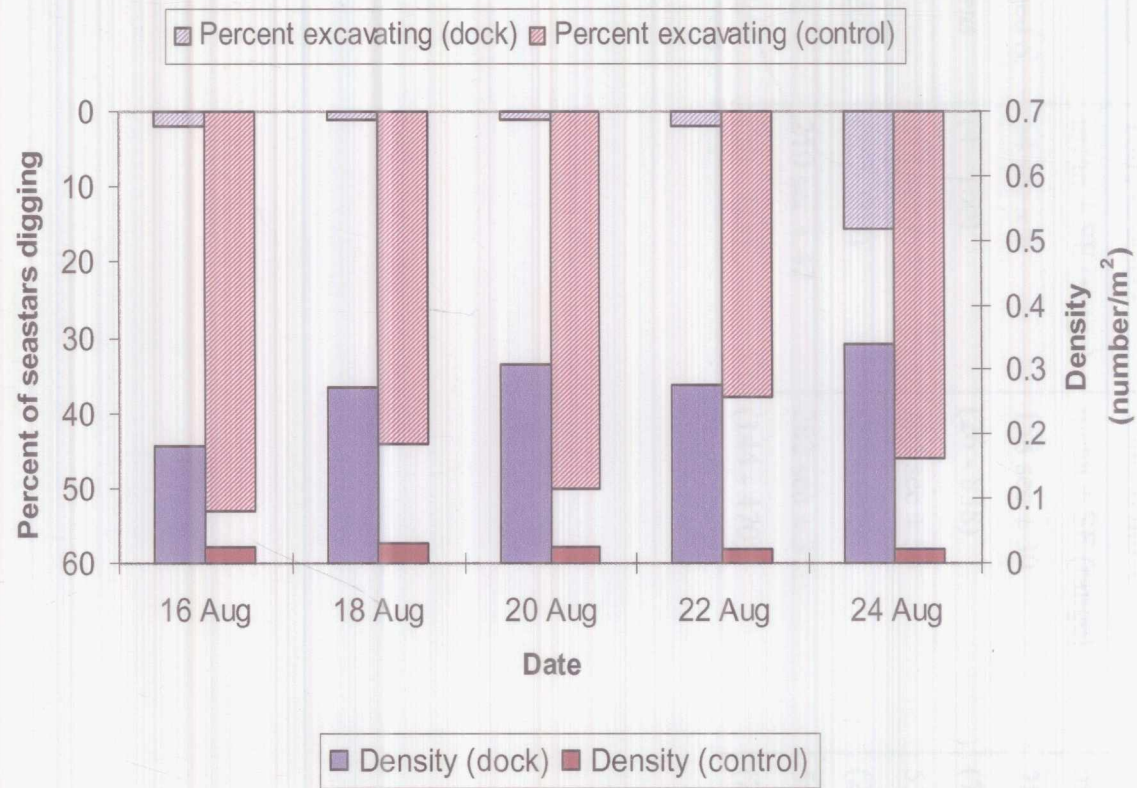


Figure 11. Density of *Pycnopodia helianthoides* (solid bars) and percent of *P. helianthoides* excavating (shaded bars) in the supplementation surveys at Jakolof dock and in the nearby control area.

Table 1. The ranges and means for the time to detect, time to move, and time to reach each of the experimental treatments (*). "Treatments" are damaged *Saxidomus giganteus** and shell control, live *S. giganteus** and shell control, and Y-maze control* (n = 30/treatment).

Treatment	Time to detect mean \pm SE (range)	Time to move mean \pm SE (range)	Time to reach mean \pm SE (range)
Damaged <i>S.</i> <i>giganteus</i>	54 sec \pm 8 (4 - 160)	158 sec \pm 30 (26 - 838)	283 sec \pm 35 (72 - 865)
Live <i>S.</i> <i>giganteus</i>	276 sec \pm 45 (25 - 605)	304 sec \pm 56 (20 - 662)	533 sec \pm 96 (250 - 658)
Y-maze controls	210 sec \pm 42 (30 - 424)	282 sec \pm 31 (144 - 470)	500 sec \pm 109 (283 - 613)

Table 2. Two-way ANOVA of the cue propagation experiment. "Treatments" are experimental and control, locations are up-current and down-current. "Moved" are seastars that moved towards the prey. "Reached" are seastars that reached the prey ($n = 6$).

		SS	Deg. of Freedom	MS	F	P
Moved	TREATMENT	0.95	1	0.95	18.63	0.0003
	LOCATION	0.86	1	0.86	16.86	0.0005
	TREATMENT*LOCATION	0.93	1	0.93	18.12	0.0004
Reached	TREATMENT	0.78	1	0.78	15.94	0.0007
	LOCATION	0.78	1	0.78	15.94	0.0007
	TREATMENT*LOCATION	0.78	1	0.78	15.94	0.0007

Table 3. One-way ANOVA in the corridor experiment. "Treatments" are damaged *Saxidomus giganteus* and live *S. giganteus*, damaged *S. giganteus* and live *S. giganteus* with a *Pycnopodia helianthoides* in an excavation, only damaged *S. giganteus* and only live *S. giganteus* (n = 15/treatment).

	SS	Deg. of Freedom	MS	F	P	R ²
Intercept	166.87	1	166.87	782.15	< 0.0001	0.76
TREATMENT	40.02	3	13.34	62.52	<0.0001	
Error	12.59	59	0.21			

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